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THE HISTORICAL AND BIOGRAPHICAL CONTEXT OF GREGORY'S DIVERTICULUM, AN UNUSUAL ORGAN IN SAND DOLLARS

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ABSTRACT. Gregory's diverticulum is a conspicuous digestive tract element found in selected sand dollar (Echinoidea: Clypeasteroida) species. This organ, a transitory structure of the juvenile organism, was named after the American zoologist Emily R. Gregory (1863–1946). Although it had been observed before by the renowned echinoid researcher and former director of the Museum of Comparative Zoology Alexander E. Agassiz, Gregory was the first to describe the organ as a distinct entity on the basis of the ubiquitous sand dollar species *Echinarachnius parma*. However, despite presenting her discovery at several national and international conferences, as well as in short papers, Gregory's find remained largely unmentioned by contemporary echinoderm researchers. With the erroneous assessment of one of the most eminent authorities on echinoid taxonomy and systematics Theodor J. Mortensen that the organ she discovered does not exist, Gregory's work seemed destined to fall into oblivion. However, in the second half of the 20th century, several unpublished master's theses provided unequivocal evidence for the existence of the organ, thus reviving interest in research on Gregory's diverticulum. The present article gives a historical overview of studies related to Gregory's diverticulum, provides the first comprehensive biography of Emily R. Gregory, describes the circumstances of the organ's discovery, and explores why the research of a female zoologist was seemingly not met with much enthusiasm during her lifetime.

KEY WORDS: Echinodermata; Emily R. Gregory; digestive tract; Alexander E. Agassiz; Hubert L. Clark; Theodor J. Mortensen; Robert T. Jackson; internal organ; sea urchin; Museum of Comparative Zoology

INTRODUCTION

The digestive tract of scutelline sand dollars (Clypeasteroida: Scutellina), a taxon of dorsoventrally flattened sea urchins (Echinodermata: Echinoidea), is characterized by the presence of Gregory's diverticulum. This internal soft tissue organ, a derivative of the digestive tract, is remarkable in several ways. First, it is a transient structure that in most

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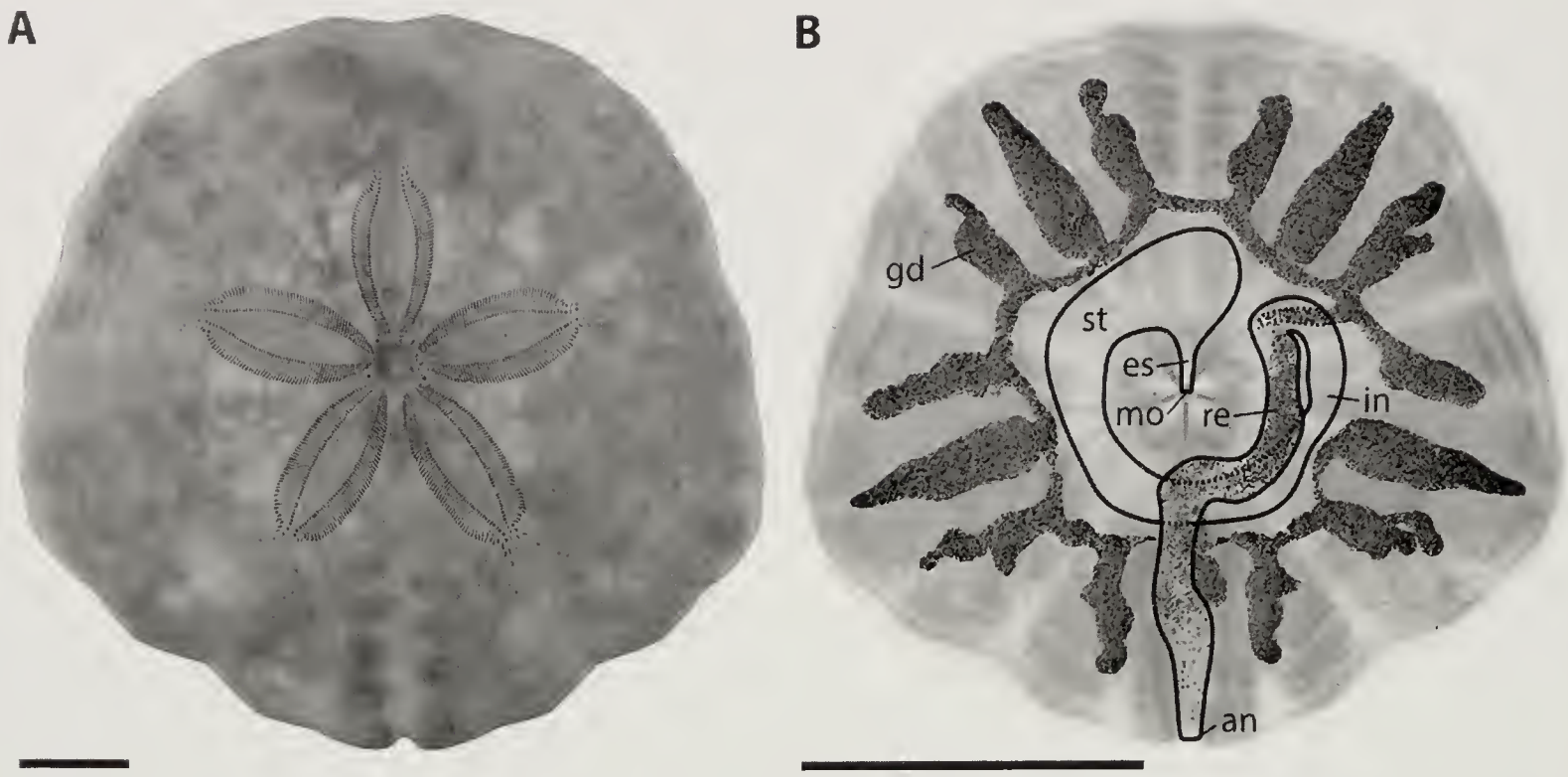

Figure 1. Morphology of Gregory's diverticulum in the scutelline sand dollar species *Scaphechinus mirabilis*. (A) Aboral view of the denuded test of an adult specimen. Image courtesy of Andreas Kroh. (B) Microcomputed tomography–based, semitransparent volume rendering of a juvenile specimen showing the sand-filled Gregory's diverticulum in relation to a schematic of the remainder of the digestive tract. Modified from Ziegler et al. (2016, fig. 1). Scale bar = 10 mm. an = anus, es = esophagus, gd = Gregory's diverticulum, in = intestine, mo = mouth, re = rectum, st = stomach.

species is present in juvenile stages only. Second, it serves the young organism in selectively storing sediment particles that are particularly dense, thereby making the individual heavier. Last, but not least, it is composed of a transparent, nonmuscular, elastic tissue with largely unknown physiological and mechanical properties.

The organ was first described by the American zoologist Emily Ray Gregory (1863–1946). In a short note, she reported on "An unnoticed organ of the Sand-dollar, *Echinarachnius parma*" (Gregory, 1905:270). By dissecting juveniles and adults of this popular marine invertebrate found along the U.S. East Coast, she had discovered "a blind-ending diverticulum of the intestine which passes around the body-cavity, giving off branches on the outer side" (Fig. 1). However, although she presented her findings during several national and international conferences, as well as in the form of short publications, contemporary echinoderm researchers largely ignored Gregory's results and ultimately rejected them. The present article explores what circumstances could have led to this misjudgment. To this end, we provide a summary of research conducted on Gregory's diverticulum, present the first comprehensive biographical sketch of Gregory, explore what experiences could have shaped her as a person, and reconstruct the circumstances of the discovery of this still enigmatic organ.

HISTORICAL OVERVIEW OF RESEARCH ON GREGORY'S DIVERTICULUM

Although an early account by Louis R. Agassiz, founder and first director of the Museum of Comparative Zoology (MCZ), briefly mentions that the digestive tract of several clypeasteroid species "est garni dans tout son trajet d'appendices ou de processus

Figure 2. First drawings of Gregory's diverticulum, all based on the sand dollar species *Echinarachnius parma*. (A) Oral view of a dissected juvenile specimen. Modified from Agassiz (1872–74, pl. 31). (B) Oral view of a dissected adult specimen. Gregory's diverticulum is present in a reduced form. Modified from MacBride (1906, fig. 244). (C) Aboral view of a dissected adult specimen. Gregory's diverticulum is present in a strongly reduced form. Modified from Coe (1912, pl. 24). gd = Gregory's diverticulum. Not to scale.

latéraux," his text and plates do not elucidate the matter any further (Agassiz, 1841:17, pls. 3, 6a, 22). Additionally, he mentioned in his manuscript the alleged presence of these appendages in *Laganum laganum,* a species now known not to possess Gregory's diverticulum (Ziegler et al., 2016). The first to provide evidence for the existence of the organ was therefore his son, Alexander E. Agassiz. In his *Revision of the Echini* (Agassiz, 1872–74), the second director of the MCZ presented a drawing of a specimen of *E. parma* with Gregory's diverticulum (Fig. 2A). However, he mistook the structure for a component of the circulatory system, labeling it the "actinal vessel on the actinal floor" (Agassiz, 1872–74:691, pl. 31). Thus, the honor of the diverticulum's discovery must be attributed to Gregory (1905), who was the first to recognize the organ's true affinity with the digestive tract. In her brief report, she hypothesized that the diverticulum's function could be "removing sand from the intestine" or "carrying it to the different parts of the body cavity" (Gregory, 1905:270). Unfortunately, her short note did not include a graphical representation of the organ. Just one year later, however, the diverticulum was pictured in *E. parma* by Ernest W. MacBride in a textbook on echinoderms (MacBride, 1906, fig. 244) as well as 6 years later by Wesley R. Coe in his report on the *Echinoderms of Connecticut* (Coe, 1912, pl. 24). However, these two authors showed the organ in its reduced state in the adult and did not identify that particular structure (Figs. 2B, C). Coincidentally, in parallel to Coe's report, a paper by Gregory (1912a:202) mentioned that the organ may still be present in the adult as a "vestigial structure."

Despite the prolific work on sand dollar morphology conducted during the first half of the 20th century by echinoderm researchers such as Hubert L. Clark, René Koehler, Theodor J. Mortensen, Lucien Cuénot, and Robert T. Jackson, it would take almost four decades for the organ to be mentioned again. However, in his fourth volume of *A Monograph of the Echinoidea*, Mortensen (1948:371) noted that "The unnoticed organ described by E. R. Gregory (1905) appears to be only the strongly widened proximal part of the intestine, the outer wall of which is conspicuously folded, as shown by Coe" (Fig. 2C). This short but definite statement concluded studies on Gregory's diverticulum for the first half of the 20th century.

Nevertheless, research on Gregory's diverticulum experienced a renaissance in the second half of the last century. In a study on the internal hard-part morphology of *Dendraster excentricus* by David M. Raup (1958, pl. 1A), the organ was documented using X-rays for the first time but yet again not identified. However, only a few years later, the presence of the diverticulum in *Mellita isometra* and *Encope grandis* was demonstrated by Carol D. Wagner (1963, p. 15, fig. 3) in her unpublished master's thesis on fossil clypeasteroids. She was also the first person to mention that the sand-filled diverticulum might serve the juvenile as "a balancing aid" and that a selection of sand grains must occur inside the gut (Wagner, 1963:16). Almost a decade later, the first thorough overview of the organ was presented, again in the form of an unpublished master's thesis (Mitchell, 1972). On the basis of his broad bibliographical, historical, and morphological survey, Branton P. Mitchell rightfully decided to name the organ after Gregory.

The groundbreaking work performed in these two theses as well as further experimental evidence then led Fu-Shiang Chia (1973) to formulate the "weight belt" hypothesis. He showed that juveniles of *D. excentricus* are capable of selectively accumulating heavy minerals in their diverticulum. Subsequently, D. Keith Serafy (1978) provided a short note on the composition of the sediment in the diverticulum of *E. parma* and Adolf Seilacher (1979:213, fig. 22) showed that a sand-filled diverticulum is also present in *Mellita quinquiesperforata* and *Mellitella stokesii*, but absent in the nonscutelline sand dollar species *Arachnoides placenta* and *Heliophora orbiculus*. A year later, Maria E. Caso (1980, figs. 110–113) presented dissected specimens of *Lanthonia longifissa* that contained considerable amounts of dark sand grains, although she did not mention this particular fact. Then, Gregory's diverticulum was briefly referred to by Chantal De Ridder and Michel Jangoux (1982:221) in the textbook *Echinoderm Nutrition*, followed by a short note from Serafy and F. Julian Fell (1985:22) on the properties of the sediment contained within the diverticulum of *E. parma*. In parallel, Chia (1985:219) presented the first and so far only histological study of Gregory's diverticulum and mentioned that "it is entirely possible that sand particles can be dissolved in situ by either acid or iron-reducing bacteria". He also mentioned the organ's absence in the nonscutelline sand dollar species *Jacksonaster depressum*.

The first evidence for the presence of Gregory's diverticulum in extinct sand dollars was, again, provided in an unpublished master's thesis; Robert A. Linder (1986:90, fig. 47) demonstrated that preferential selection of heavy minerals must have occurred in the fossil clypeasteroid genus *Kewia*, as well. A year later, Malcolm Telford and Richard J. Mooi (1987:32) presented an X-ray image of *Mellita* with a well-developed Gregory's diverticulum, and Linder gave further evidence for the presence of the organ in *Kewia* (Linder, 1988; Linder et al., 1988:945, fig. 5). In his study on the function of lunules, Telford (1988; fig. 4) then showed X-ray images of a sand-filled diverticulum in *Mellita isometra*. A few years later, Anne M. F. Moore and Olaf Ellers (1993:254, fig. 1) mentioned that the "calcite belt" formed by the adult sand dollar's endoskeleton might at a given point during ontogeny replace the presumed "weight belt" function of the sand-filled diverticulum. The number of species known to possess Gregory's diverticulum was later expanded by Chang-Po Chen and Bih-Yun Chen (1994), who showed that *Sinaechinocyamus mai* and *Scaphechinus mirabilis* possess Gregory's diverticulum. These two authors also report-

ed that the former, paedomorphic species retains a sand-filled organ into adulthood.

The first broad survey of Gregory's diverticulum was presented by Mooi and Chen (1996), who described the distribution of the organ in multiple extant as well as fossil sand dollar taxa. Their analyses showed that the organ most likely constitutes an apomorphy of the clypeasteroid clade Scutellina. One year later, a detailed account of Gregory's diverticulum in *M. quinquiesperforata* was presented by Carlos A. Borzone and colleagues (1997), who provided schematic drawings and photographs of the organ in a comprehensive size series. In his review of the function of eponymous structures in echinoderms, John M. Lawrence (2001:1254) then gave a brief summary of studies on Gregory's diverticulum and hypothesized that the selection of heavy particles into the diverticulum could be caused by differential movement of light and heavy sand particles through the digestive tract.

Additional photographic evidence for the presence of the organ in *M. stokesii* was provided by Heinke Schultz (2005, fig. 653), and James P. Swigart (2006:7), in his unpublished master's thesis, briefly mentioned the presence of Gregory's diverticulum in a further species, *Mellita tenuis*. Using microcomputed tomography, Louis G. Zachos (2006) showed that the organ is also present in *Encope michelini*, and Susan E. Hilber and Lawrence (2009) reiterated the hypothesis that differential movement of light and heavy sediment particles could occur within the gut. Further photographic evidence for the presence of Gregory's diverticulum in *M. stokesii*, *S. mai*, and *Scaphechinus tenuis* was later provided by Alexander Ziegler and colleagues (2010, fig. 7) in a study focusing on a separate digestive tract structure in sea urchins. In parallel to this article, Thomas Carefoot introduced a short exercise on Gregory's diverticulum in his online educational tool on *D. excentricus* (Carefoot, 2010).

The more recent studies on aspects of the organ are two reports presented by Yury N. Elkin and colleagues. These studies focus on *S. mirabilis* and provide information on sediment composition within its diverticulum and the substrate (Elkin et al. 2012) as well as a discussion of the potential elimination of the diverticular content through bacterial symbionts (Elkin et al. 2013). These reports were complemented by two studies conducted by Andrey A. Begun and colleagues that report on food preferences of the two sand dollar species *E. parma* and *S. mirabilis* (Begun et al., 2014; Begun and Elkin, 2015). The latest research on Gregory's diverticulum was performed by Ziegler et al. (2015, 2016), who presented a comprehensive descriptive and visual overview of the organ's morphology and evolutionary history, including the discovery of two distinct morphotypes of the organ (Fig. 3).

Given that Gregory's find was first ignored and later rejected by her peers (Mortensen, 1948), the fact that the organ is now being mentioned in a standard textbook on invertebrate zoology (Brusca et al., 2016:989) would certainly have made her very proud.

BIOGRAPHY OF EMILY RAY GREGORY

Early life and school

Emily R. Gregory was born on 1 November 1863 in Philadelphia, Pennsylvania (Creese, 2000). She was the daughter of Mary (Jones) and Henry D. Gregory, Ph.D., and had five sisters and two brothers. Henry D. Gregory was a scholar and puritan Presbyterian, whose grandfather had come to the United States to fight in the American War on Independence under General Lafayette. Emily's older brother, Caspar R.

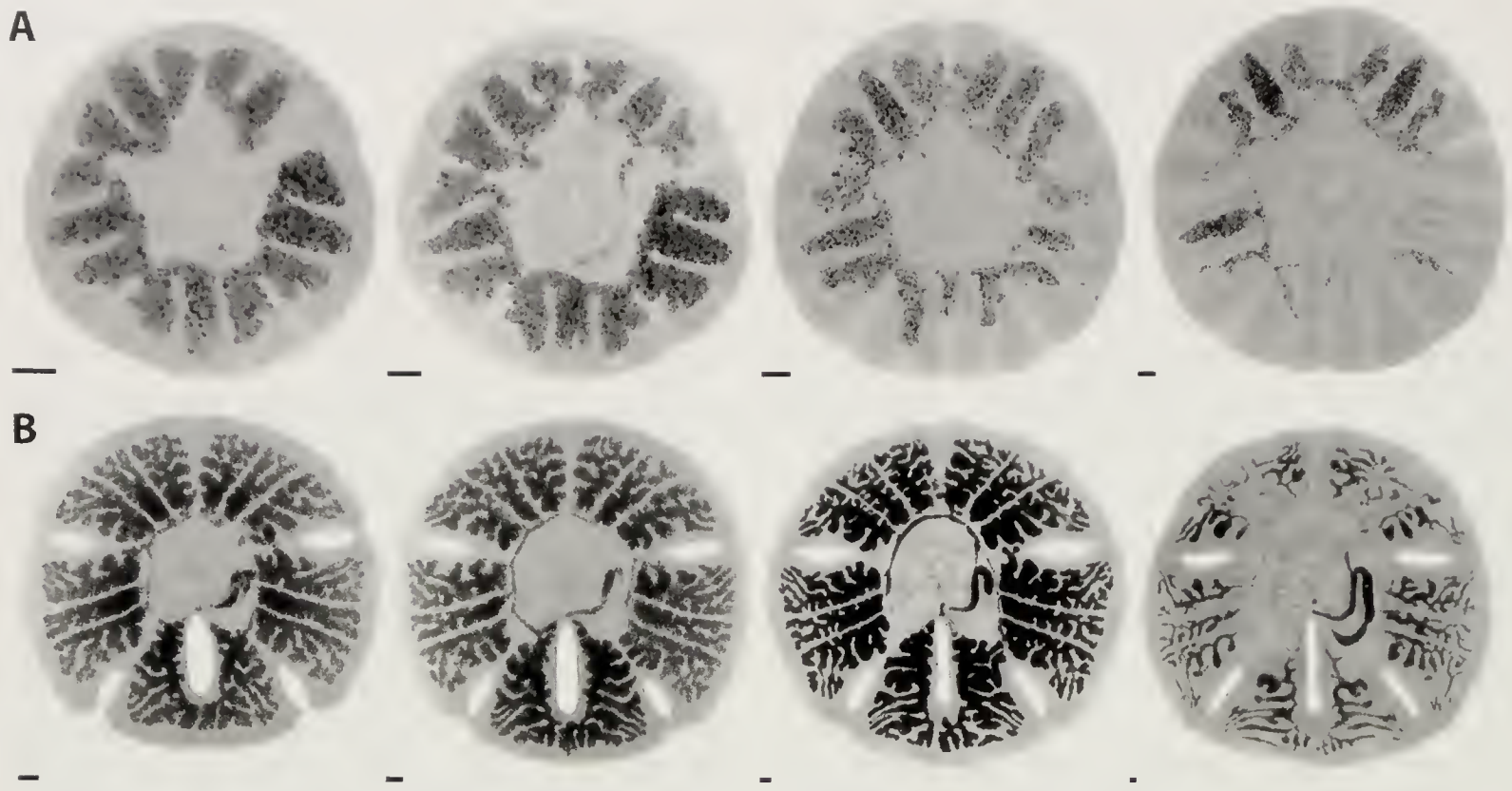

Figure 3. Variation in shape and size of Gregory's diverticulum. This figure depicts X-ray images of (A) *Echinarachnius parma* (MCZ 2613) and (B) *Lanthonia longifissa* (MCZ 2626) illustrating the two morphotypes of the organ. Additionally, these two size series show the consecutive reduction of the organ during ontogeny. Modified from Ziegler et al. (2016, figs. 3, 7). Scale bar = 1 mm.

Gregory became a respected theologian who moved to Saxony in 1873, where he obtained his first doctoral degree at the Universität Leipzig in 1896. He is best known for his work on New Testament textual criticism and for creating a classification system for biblical manuscripts still in use today (Anonymous, 1911). Caspar's and Emily's father was working as a teacher in various schools and colleges on the U.S. East Coast. In 1875, he became principal of Blair Presbyterial Academy in Blairstown, New Jersey, where part of his family was living with him on campus (Howers, 1935). Emily attended this school, receiving a comprehensive high school education in music, in particular piano and singing (Ogilvie, 1993).

Academic education

At the age of 17, Emily R. Gregory was sent to Wellesley College in Massachusetts, where from 1880 to 1885 she participated in the Classical Music Course (Fig. 4). She obtained her B.A. degree in 1885 at the age of 21 and began to work as a teacher in two girls' schools in Philadelphia, Miss Mitchell's School for Girls (1885–1886) and Miss Case's and Miss Hallowell's School (1887–1888). During those years, she developed an interest in biology and decided to enroll in the graduate program for zoology at the University of Pennsylvania in Philadelphia (1889–1892). However, to support her studies, she had to resume her original vocation (Ogilvie and Harvey, 2000) and so first worked as a teacher at the Southern Home School in Baltimore, Maryland (1893–1894) and then as a professor of biology at Milwaukee College in Wisconsin (1894–1895). In 1896, at the age of 32, she obtained her master's degree in zoology from the University of Pennsylvania. In parallel, she repeatedly attended summer courses at the Marine Biological Laboratory (MBL) in Woods Hole, Massachusetts (Fig. 5). There,

she came in contact with the MBL's founder and former assistant at the MCZ, Charles O. Whitman (Creese, 2000), who offered Gregory the opportunity to conduct her Ph.D. studies in his lab. In 1895, about 1 year before obtaining her master's degree, she was accepted as a fellow and subsequently as an assistant in zoology at Whitman's lab at the University of Chicago in Illinois (1895–1899). Her work there was conducted under the guidance of William M. Wheeler, who later became a professor at Harvard's Bussey Institute. During her Ph.D. studies, Gregory embarked on occasional field trips that involved collecting freshwater turtle eggs east of Chicago at Turkey Lake, Indiana (1897–1898). Her Ph.D. thesis on the development of excretory systems in turtles was presented in 1899 and published the following year (Gregory, 1900).

Career in academia

After finishing her doctoral degree, Gregory traveled to Europe to conduct research at the Stazione Zoologica Anton Dohrn in Naples, Italy (1899–1900). This private institute had been founded in 1872 to provide research space for scientists interested in marine biology. The station had laboratories ("tables"), a library, and support staff. Ida H. Hyde, an American physiologist who had received her doctoral degree from the Kaiser-Wilhelm-Universität Straßburg against considerable resistance, was invited to the station in 1897 to occupy the table of the Ruprecht-Karls-Universität Heidelberg. Following this experience, she "resolved upon returning to the United States to do all in [her] power to enable eligible women scientists to avail themselves of the laboratory's unexcelled opportunities" (Sloan, 1978:210). Hyde was instrumental in raising the fee to establish the American Women's Table sponsored by the Naples

Figure 4. Photograph of Emily Ray Gregory dated 1884. Image courtesy of Wellesley College Archives.

Table Association for Promoting Research by Women. It was this exact table that Gregory held during her time in Naples.

While in Europe, Gregory also spent some time at the Université de Grenoble in France and traveled to Saxony to visit her brother Caspar and his family in Leipzig (Gregory, 1846–1917). After returning from Europe, She presumably spent some time working as a professor at the newly established National Cathedral School in Washington, D.C. (1901). However, for the rest of the decade Gregory worked as a professor of biology at Wells College in Aurora, New York (1901–1909). Apparently, she was looking forward to her time there, for in a letter dated 27 October 1901 she wrote to her brother Caspar: "I will never be illustrious like yourself, but here is work worth doing for

Figure 5. Participants and instructors of the course on botany held in the summer of 1894 at the Marine Biological Laboratory. Emily Ray Gregory is wearing a striped blouse. Image courtesy of Marine Biological Laboratory Archives.

which I am prepared and which is not too heavy for my strength" (Gregory, 1846–1917).

During the summers of these years, Gregory frequently visited the Harpswell Laboratory in South Harpswell, Maine, where she conducted research on marine invertebrates, including sand dollars. On leave of absence from Wells College (Anonymous, 1909), she then worked as a visiting professor of biology, physiology, and hygiene at the American College for Girls in Constantinople (1909–1911), then the capital of the Ottoman Empire. In letters to her brother Caspar, she complained of the heat and of cholera rampant in the city (Gregory, 1846–1917). To help alleviate this situation, Gregory organized lectures on personal hygiene for Turkish women and American expatriates, an experience that probably marked her increasing interest in social issues. Determined to devote all her time to sociological work, she returned to the United States in 1912 with hopes of raising money and finding recruits to establish a charity headquarters in Turkey (Anonymous, 1912a). However, these plans never came to fruition because of political turmoil in Turkey. Therefore, Gregory resumed her work as a professor of biology, first at the Municipal University of Akron in Ohio (1913–1915), then for a short time at her old Alma mater, Wellesley College (Fig. 6), and finally at Sweet Briar College in Virginia (1915–1917). During these years she apparently could not resist following her new

Figure 6. Photograph of Emily Ray Gregory dated 1914. Image courtesy of The University of Akron Archival Services.

interest in preventive medicine, and so in parallel to her work as a professor of biology, Gregory took courses at the medical faculty of the University of Pennsylvania in Philadelphia (1915–1916).

Career in administration

Toward the end of the First World War, at the age of 55, Gregory abruptly ended her career in academia. This step may have been precipitated by the death of her brother Caspar, who had become a naturalized citizen of Saxony in 1881 and enlisted in the Saxon Army when the war broke out; aged 68, he was the oldest volunteer of the German Empire. We know from a letter that Emily wrote to him in 1915 that she was upset about his participation in the war. She told him that he should not believe all he hears about the United States and that allegations would be "not only false but outrageous, and malicious deceit." In reference to the fighting, she also spoke of the "incredible, unspeakable slaughter" (Gregory, 1846–1917). Tragically, Emily's dark sense of foreboding proved true, and in 1917, *Leutnant* Caspar R. Gregory died of wounds on the Western Front. Given how close they had been, Emily must have been devastated. Having given up her academic career, she first worked as a special research investigator at the U.S. War Trade Board (1918–1919) and later as a first class clerk at the U.S. Department of the Treasury in Washington, D.C. (1919–1924), where she finally retired at the age of 61.

Later life

Emily R. Gregory was never married and did not have any children, thus giving her ample time and energy to entertain various hobbies. Apart from her obvious interest in the life sciences, her favorite pastimes were "walking, skating, travel, music, painting, sculpture, flowers, nature, all outdoors" (Howers, 1935:220). Her interest in music also persisted throughout her life, as evidenced by a letter she wrote to her brother Caspar's wife Lucy on 22 April 1900, in which she mentioned that she might have left her musical notes at their house in Leipzig during her visit to Europe (Gregory, 1846–1917). Following her retirement from the U.S. Department of the Treasury in 1924, Gregory moved back to her hometown Philadelphia, where for more than two decades she remained active with regard to her social and political commitments. On 18 January 1946, Emily Ray Gregory, Ph.D., passed away in her home at the age of 82. Shortly after her death, an obituary was published in the *New York Times* (Anonymous, 1946).

EMILY RAY GREGORY'S ACADEMIC AND PUBLIC ACTIONS

Teaching and research

Emily R. Gregory's teaching encompassed a diverse array of topics in biology, such as

botany, invertebrate zoology, comparative zoology of vertebrates, physiology, vertebrate embryology, and methods in histology, but she also taught medical courses, such as advanced hygiene and eugenics. In addition to her classroom teaching, Gregory also gave practical lessons (e.g., "Lectures on Hygiene for Freshmen Women") that included "Gymnasium work" (Anonymous, 1914:103).

With regard to her zoological research, Gregory's residences at the University of Chicago (1895–1899) and Wells College (1901–1909) were her most productive periods. Her published scientific work includes studies on vertebrate embryology, sand dollar morphology and anatomy, and methodological advances. Additionally, she published a few articles on educational topics, some of them after her retirement. However, Gregory's overall scientific output was comparatively low, as illustrated by the list of publications authored by her given at the end of this article.

Political activism

During her time as a student at Wellesley College, Gregory had become a member of the sorority Kappa Kappa Gamma. In line with her general interest in social issues, she was active in various other organizations that promoted women in science, including the American Association of University Women and the International Federation of University Women. However, in 1901 she also became a fellow of the American Association for the Advancement of Science (AAAS), which had, at that time, almost exclusively male members.

In addition to her dedication to educational topics, Gregory was heavily engaged in community work and advocated sociopolitical issues such as preventive medicine and welfare. For example, she supported the smoking ban at Wellesley College and wrote in the college's monthly magazine: "let me congratulate you on the sane and sensible ban which you have placed on smoking," an activity that according to her "lessens the mental acumen and blunts the moral tone of the users and markedly that of their children" (Gregory, 1926). Further interests of hers were public affairs, government, citizenship, and crime prevention (Howers, 1935). To achieve her social and political goals, she supported various organizations, including the New Century Guild, the League for the Hard of Hearing, the Republican Women of Pennsylvania, the League of Women Voters, and the Philadelphia Conference on Government (Ogilvie and Harvey, 2003).

As a politicized woman, Gregory presumably sympathized with the suffragist movement. She was acquainted with Jane Addams (Gregory, 1912b), who was a strong advocate for peace and of the right for female citizens to vote. Addams felt that women would be able to push through the social reforms that she wanted to see (Yans and Shin, 2013). However, if Gregory ever expressed suffragist views to her male scientific colleagues, this would presumably not have endeared her to them, for we know that at least some of them were strongly opposed to giving the franchise to women. For instance, Robert T. Jackson, curator of fossil echinoderms at the MCZ, expressed his strong opposition to the suffragist movement in a letter to Francis A. Bather of the British Museum of Natural History. Like Jackson, Bather worked on echinoids and was Jackson's frequent correspondent, but in this letter he gently chides Jackson for his attitude towards the suffragists, in which Jackson apparently referred to their "vandalism of England's most precious monuments" (Jackson, 1854–1935). However, Bather pointed out that the suffragists in

England had not done any actual damage and that their activities were "aimed only to frighten the public and to give warning of what might happen rather than for the moment to commit actual damage ... in your country, as our Press is never tired of telling us, the women suffragists behave very differently .... There may be another way of treating these women than that which you suggest" (Jackson, 1854–1935). It would be interesting to know how Jackson had suggested that the suffragists be treated, but his outgoing letters to Bather are unfortunately not preserved. Gregory certainly knew Jackson through their joint membership in the AAAS as well as through his teaching at the MBL, and probably others in the male scientific community shared his feelings about votes for women.

Nonetheless, or maybe as a consequence, Gregory did not hesitate to speak her mind. For instance, she wrote a rather stinging rebuke to Jane Addams for her support of Theodore Roosevelt Jr.'s "so-called Progressive Party," as Gregory (1912b) put it. In her letter to Addams, she said in part: "I am bewildered and amazed that [anyone] could so have pulled wool over your eyes or raised such a cloud of dust as to becloud that vision and make it possible for you to enter or at least remain in the Third Term Party—for such it really is" (Gregory, 1912b). This was strong language to use to someone of Addams' stature, especially since there is no evidence that the two women were particularly close.

Female life in academia

Further evidence suggests that many of Gregory's male colleagues opposed, in varying degrees, welcoming women into the academic world. For example, Ida H. Hyde, who was instrumental in establishing the American Women's Table in Naples and who must have met Gregory at the MBL in the last decade of the 19th century, had some interesting correspondence regarding female scientists with F. Anton Dohrn, the Stazione's founder. Dohrn apparently was conflicted; although he had supported female scientists like Hyde at his marine station, he still held Victorian views of women's primary role (i.e., as wives and mothers). The correspondence between him and Hyde is revealing; on 20 April 1897, he wrote to Hyde: "Let me openly and sincerely confess that it has taken long years to persuade or rather convince me that the modern movement in favor of women's emancipation is a sound one." Despite his initial reservation, he concluded that "there is one part of it, for which I have not hesitated to feel and confess a strong sympathy, that is the throwing open to women the pursuit of science and the higher intellectual training" (Sloan, 1978:212).

Similar to Hyde and Gregory, other contemporary female scientists also experienced difficulties fitting into academia. A further example is the American zoologist Julia B. Platt, one of the first women neuroscientists. She was slightly older than Gregory, but their paths must have crossed occasionally, most likely in Chicago, where Platt was also working under the guidance of Charles O. Whitman. Platt's work in comparative embryology was controversial, as she identified ectodermic cells in embryos of salamanders that give rise to head cartilage, evidence that challenged the then popular germ layer theory. Although Platt's findings certainly had more cachet than Gregory's discovery, they were also rejected by her contemporaries but, similar to Gregory's diverticulum, have been confirmed over time. Another parallel with Gregory is that there are clear indications that Platt was outspoken and did not hesitate to criticize colleagues (Platt, 1889, 1898). For example,

Whitman wrote to F. Anton Dohrn in 1891 stating that "Miss Platt is, by the way, a little fond of talk, but I hope she will not prove troublesome to you" (Zottoli and Seyfarth, 1994:101). Although her experience and publishing record were outstanding, Platt was unable to find what she considered a suitable position after completing her doctorate. Perhaps her outspokenness contributed to this, as may have been the case also with Gregory. Platt withdrew from academia to immerse herself in social and public affairs, as did Gregory at a later stage in her career.

THE CIRCUMSTANCES OF EMILY RAY GREGORY'S DISCOVERY

Research at marine laboratories

Despite the focus of her Ph.D. thesis on embryological aspects of freshwater turtles, Gregory was a frequent visitor at marine stations, in particular the MBL during summers (1893–1900, 1915–1918). After receiving instruction, she later occupied a private room and also became a corporation member (MBL Annual Reports 1893–1899, 1915–1918). At the MBL in Woods Hole, Gregory became acquainted with several researchers who would be instrumental for her professional advancement. These included her later Ph.D. hosts at the University of Chicago, Charles O. Whitman and William M. Wheeler. Further likely acquaintances at MBL were Robert T. Jackson, who was giving lectures as an instructor in zoology during the summers from 1896 to 1899, as well as Hubert L. Clark, who in 1898 and 1899 was working at the MBL on his book *Echinoderms of the Woods Hole Region* (Clark, 1904). Additionally, Ida H. Hyde had started to work there in 1891 as an instructor in embryology. Given the scientific background of these academics, it is very likely that Gregory was introduced by them to some of the topics on which she would later focus her research, in particular embryology and marine invertebrate anatomy.

The objective of her work at the Stazione Zoologica Anton Dohrn (1899–1900) has not been passed on, but her studies on *E. parma* must have been conducted at Harpswell Laboratory. This small marine station was located on Casco Bay, where large tidal flats could be found right in front of the laboratory. Since its inception in 1898, the station was open summers from June until September. In his report on the working conditions and surroundings of the laboratory, the American zoologist Max W. Morse (1909:510) notes that "On shallow banks of sand exposed entirely at low tide *Echinarachnius parma* may be collected in quantities, and with great ease."

The Harpswell Laboratory started out in South Harpswell, Maine as the Tufts College Laboratory but was later relocated to Bar Harbor, Maine, where since 1921 it has been known as the Mt. Desert Island Biological Laboratory (Evans, 2015). Initially, the station in South Harpswell was a wooden, one-story building with 16 windows (Fig. 7A). A single large laboratory space was broken into smaller rooms that were more like cubicles than separate rooms (Fig. 7B). Clearly, all researchers working there must have had extensive contact with each other. Additionally, the first director, John S. Kingsley, and his wife were very hospitable and often entertained the visiting scientists at their private cottage right next to the station for various events, including dinner (Williams, 1985). There, if she had not already known them, Gregory met the influential American zoologists George A. Bates, Henry B. Bigelow, Ulric Dahlgren, and Herbert V. Neal, among others. A list of visitors shows that Gregory was there during the summers

Figure 7. The Harpswell Laboratory in South Harpswell, Maine. (A) The laboratory, looking southeast. Casco Bay is located directly behind the fence that can be seen in the background. A large beach with tidal flats is located just to the right. (B) The interior of the laboratory looking north. Modified from Morse (1909, figs. 1, 2).

of 1898, 1901, 1903, 1904, 1907, and 1908 (Williams, 1985).

Participation in meetings

To present her data on *E. parma* gathered at Harpswell Laboratory, Gregory attended several national and international meetings. In December 1904, she read her paper on the discovery of the diverticulum during the session of Section F (Zoology) at the AAAS meeting in Philadelphia (Howard, 1905:504). The abstract-like, short note reporting her discovery was published the following year in *Science* (Gregory, 1905). In August 1907, Gregory attended the 7th International Zoological Congress, held in Boston, Massachusetts, under the presidency of Alexander E. Agassiz (Anonymous, 1912b). At this meeting, she read a paper on the morphology and anatomy of various hard and soft parts of *E. parma* but also publicly showed a number of microscopic preparations, presumably of the diverticulum she had discovered a few years earlier (Anonymous, 1912b:961). Apart from Agassiz, further participants at this meeting with a research focus on echinoderms were Wesley R. Coe and Lucien Cuénot (Anonymous, 1912b). Gregory's conference paper was published in the meeting's proceedings a few years later (Gregory, 1912a). In December 1907, just half a year after the congress in Boston, she participated in a further meeting of the AAAS, this time held in Chicago. Here, she presented her third paper on *E. parma*, which described selected skeletal parts of the organism (Gregory, 1908).

Reception of Gregory's discovery

Despite the publication of her results in respected scientific journals—even if only in the form of short notes—and the presentation of her results during national and international meetings, Gregory's work on *E. parma* was not cited by her peers. This is surprising, given that several of Gregory's papers were listed in both *The Zoological Record* and the *Zoologischer Jahresbericht*, which at the time were the principal sources of information for publications on a given zoological taxon. However, before and around Mortensen's (1948) rejection of the existence of Gregory's diverticulum, no other echinoderm specialist mentioned the newfound organ in papers involving either the morphology, taxonomy, or systematics of extant as well as fossil sand dollars (Clark, 1911, 1914, 1925, 1940, 1946, 1948; Coe, 1912; Jackson, 1912, 1913, 1914, 1922; Koehler, 1922; Mortensen, 1927; Parker,

1927; Ikeda, 1935, 1936; Nisiyama 1940–41; Cuénot, 1948). This is particularly surprising because the sand-filled diverticulum can be seen in many extant species with the naked eye right through the calcified test (Schultz, 2005; Elkin et al., 2012).

Apparently, Gregory was not unaware of the fact that her work was not recognized and so, in her fourth contribution focusing on *E. parma* she wrote in the opening statement that "Other students of Echinoderms seemed unwilling to accept the evidence of my eyes or of their own, in observations on the living specimen in its normal state" (Gregory, 1911:323). In that same article, after the presentation of her results, she goes on to say: "As I was unable to fix or photograph my preparations, the observations were verified by Dr. H. V. Neal of Knox College, who was in charge of the Harpswell Laboratory where the experiments were made, and by Dr. G. A. Bates of Tufts College and others. They were reported orally to Dr. Hubert Lyman Clark of the Museum of Comparative Zoology of Harvard College on September 23rd, 1908" (Gregory, 1911:326). Hubert L. Clark was curator of echinoderms at the MCZ from 1905 to 1947, and during Gregory's lifetime he was certainly one of the most important gatekeepers for sand dollar–based research intended for publication. Apparently, this time Gregory wanted to make sure that he and other contemporary echinoderm scientists took notice of her results—apparently without success.

Even more remarkably, Gregory's discovery was also not referred to by the female zoologist Libbie H. Hyman in her thoroughly researched compendium on sea urchins and other echinoderm taxa (Hyman, 1955). Although Hyman cited two of Gregory's articles in this particular book as well as in a paper on sand dollar biology published a few years later (Hyman, 1958), she did not mention the new-found diverticulum. It is entirely possible that Hyman decided not to do so because of Mortensen's (1948) negative but erroneous assessment.

CONCLUDING REMARKS

It was certainly generally difficult for a female scientist to gain recognition for her research in the late 19th and early 20th centuries. However, although Gregory worked hard to achieve her academic and societal goals, she apparently never integrated into the predominantly male academic world. While most female biologists of her time tended to stay at one institution throughout their careers—often women's colleges or natural history museums—Gregory moved around often, which presumably did not help her to advance professionally. She probably assumed, at least initially, that fellow scientists would accept her observation of the diverticulum that now bears her name. It must have been very galling for her when they ignored it. However, Gregory seems to have been outspoken and apparently did not hesitate to express her opinions, which might have antagonized some of her male colleagues.

But the question remains: Why did none of Gregory's contemporaries cite her work? The fact that she was a woman does not alone account for the apparent neglect of her achievement, because the work of other women in the same field was often acknowledged, if only peripherally. One example of a successful woman in echinoderm research was Elisabeth Deichmann, who in the first half of the 20th century was working as a curator of marine invertebrates at the MCZ and who was widely respected (Levi, 1976; Pawson and Vance, 2010). Did renowned echinoderm researchers deliberately ignore Gregory's findings because she spoke her mind and at a later point criticized male

colleagues who did not acknowledge her findings? Or was her discovery judged as too insignificant to merit citation or further study?

We might never know the answer to these questions. However, in that era, women who did not hesitate to disagree with their male colleagues very likely encountered more difficulties than their more accommodating peers. Fortunately, the situation has changed considerably since then and the discovery of a new organ is bound to result in recognition by the scientific community, independent of gender.

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